PHYSIOLOGICAL STUDIES IN DROUGHT RESISTANCE. I. TECHNIQUE.

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(Two Text-figures.)

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Introduction.

Some ten years ago the study of drought resistance received a great impetus from the work of Maximov and his colleagues (1929, 1931). It was established that drought resistance was not usually concerned with conservation of water or with economy of transpiration, but rather with ability to endure wilting unharmed. There are indeed instances where a plant survives drought by virtue of its extensive root system, or its succulent water storage tissue; but the most common cause of xerophytism is a property of the protoplasm to withstand desiccation, analogous perhaps to the drought resisting properties of a resting seed. Zalenski (1904), Alexandrov (1922), Tumanov (1927), and others showed that for certain plants there is a close correlation between anatomical structure and drought resistance, but this xeromorphy is a consequence of dry conditions rather than the means of overcoming them.

All these researches gave a fresh orientation to work on drought resistance, and there has followed a steady flow of papers, especially from the U.S.S.R. and the U.S.A.; a critical summary of these will be presented in a later contribution to this series. One of the facts which emerge from this copious literature is that the current methods of measuring drought resistance are unsatisfactory. The wilting of the detached leaf, a criterion used by Paltridge and Mair in this country (1936), bears no relation to xerophytism. The percentage mortality after exposure to a hot, dry draught (Shirley, 1934) neglects the fact that actual death from drought is uncommon. An arrested development of the plant is the more usual response to drought, and no simple relation has yet been demonstrated between mortality rate and drought resistance in the sense understood by the agriculturist.

In 1931 one of the present writers (E.A.) carried out some preliminary experiments on a method of estimating drought resistance which does not involve the death of the plant, namely, by measuring the rate of growth immediately after a period of drought is over. A plant which succumbs to drought does not necessarily die, but it does not resume growth when the rain comes; resumption of growth is therefore an appropriate measure of drought resistance.

Studies are now in progress in this laboratory which apply this technique to the analysis of the effects of mineral fertilizers on drought resistance. The purpose of the present paper is to set out some preliminary data which illustrate the use of the new technique. The data refer to an experiment on the effect of nitrogen on the drought resistance of two varieties of oats, Algerian and Fulghum. Algerian, which is reputed to be drought resistant, is grown on the tablelands of New South Wales, and Fulghum is grown on the coast.

Method.

The plants were grown in sand cultures in a plant-house from March to June, 1939. Forty-eight unglazed earthenware pots, ten inches in diameter, were filled with washed river sand overlying a base of road metal and pot crocks for drainage. The pots were arranged in two blocks in the plant-house. Each block contained eight randomized treatments, and there were in each block three pots to each treatment. The plan of the experiment was as follows:

Two varieties (Algerian, A, and Fulghum, B).

Two levels of manuring (high nitrogen, +N, and low nitrogen, −N).

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Two water treatments (normal watering, C, and drought, D).
Two blocks in the plant-house.
Three replicate pots in each treatment.

The use of pots ensured that any differences in drought resistance due to root development were eliminated. Errors due to variation of light and temperature through the plant-house were minimized by changing the position of the pots within blocks twice weekly. During the experiment temperature and humidity in the plant-house were recorded with a thermohydrograph; a summary of the readings is presented in Table 1,

TABLE 1.

Summary of Temperature and Humidity Readings in Plant-house and Details of Experiment on Drought Resistance.

Date.	Weekly Temp. Min.	Weekly Temp. Max.	Weekly Humidity. Min.	Weekly Humidity. Max.	Height[1] Measured.	Fertilizer Applied.	Remarks.
Mar. 8 ..							Grain soaked in distilled water.
,, 9 ..							Grain sown in pots, watered with tap water.
,, 13–19	70	100	50	98			
,, 20–26	60	96	58	100			
,, 21					x	x[5]	1–2 leaves visible, height measured to tip of highest leaf.
,, 23 ..							Plants reduced to 12 per pot.[2]
,, 27– Apr. 2..	64	91	38	99			
Mar. 30 ..					x	x	3 leaves ; manurial and varietal effects visible.
Apr. 3–9	68	98	50	100			All plants sprayed with nicotine and soap solution.
,, 6 ..							All pots watered. DROUGHT BEGUN.
,, 10–16	63	100	51	100			
,, 11 ..					x		Dry weight samples. N-deficiency symptoms evident.
,, 12 ..							Controls watered.[3]
,, 17–23	56	97	51	100			
,, 20 ..					x		Inflorescences and tillers appear in B+ND.[4]
,, 22 ..					x		
,, 24–30	54	94	34	99			
,, 27 ..					x		Inflorescences in all treatments of B ; none in A.[4]
May 1–7	59	95	59	100			Still adequate water in −ND plants (guttation).
,, 4 ..					x		
,, 8–15	56	99	55	100			
,, 11 ..					x		Evidence of leaching in +NC.
,, 12 ..							Dry weight samples taken.
,, 13 ..						x	DROUGHT BROKEN. Nitrogen applied to all pots.
,, 14 ..					x		Heights measured at frequent intervals till June 19 (for dates see Text-figure 1).
,, 16–21	70	94	80	100	(x)		
,, 18 ..					x		Tillering begun in all treatments ; A later than B.
,, 22–28	58	90	57	97	(x)		
,, 24 ..						x	Nitrogen supplied to all pots.
,, 29– June 4	60	84	75	96	(x)		
June 5–11	58	84	71	96	(x)		
,, 12–18	62	90	78	100	(x)		
,, 15 ..						x	Nitrogen supplied to all pots.
,, 19–25	60	93	59	94			

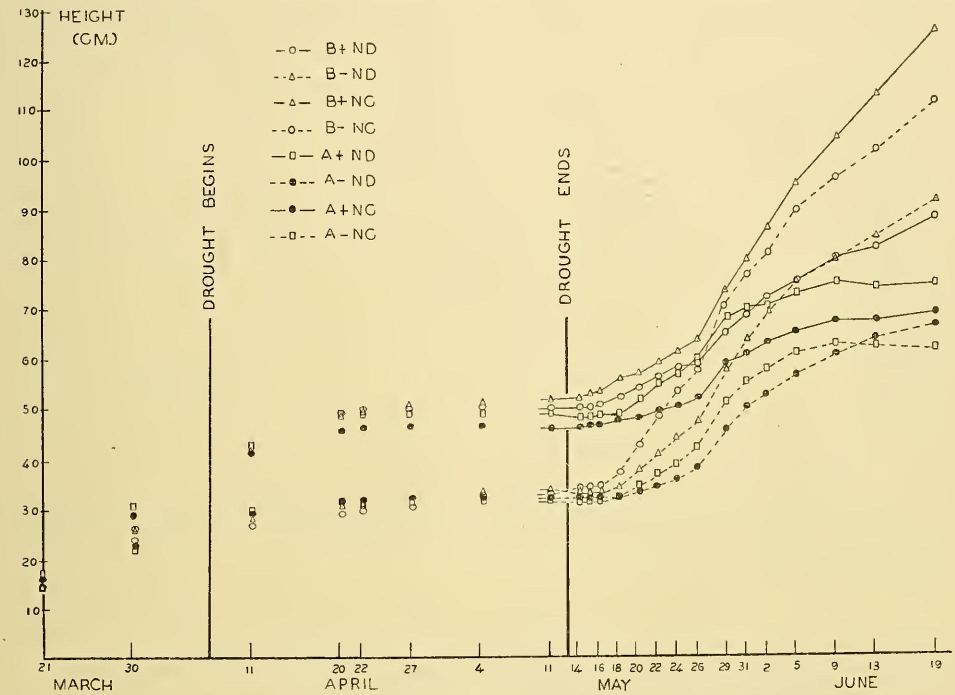
(x) means that more than one measurement was taken in the week.
[1] This includes tillers present.
[2] Plants left of average size for each variety.
[3] Water was added whenever necessary after this date.
[4] B = Fulghum, A = Algerian ; D = drought treatment ; +N = high nitrogen.
[5] The composition of the fertilizers was as follows :

	Gm. per Pot. High Nitrogen. 21.iii, 30.iii	Gm. per Pot. Low Nitrogen. 21.iii	Gm. per Pot. Low Nitrogen. 30.iii	Gm. per Pot. 13.v, 24.v, 15.vi
Nitrogen as $Ca(NO_3)_2$	0·042	0·0013	0·0053	0·021
Potassium as $KH_2(PO_3)_3$	0·029	0·029	0·029	0·029
Magnesium as $MgSO_4$	0·018	0·018	0·018	0·018
Calcium as $CaSO_4$	0·000	0·058	0·052	0·030

together with details as to the procedure of the experiment. At the close of the experiment data were obtained on the water contents of, and rate of water loss from, plants under the different treatments. These data are too inconclusive to merit discussion at this stage.

Discussion.

The data on heights of plants are presented graphically in Text-figure 1. At the onset of the drought the plants fell into two classes in respect of size: those with adequate nitrogen and those starved of nitrogen. From 6th April to 14th May there was little growth in any of the plants, whether subjected to drought or not. It was



Text-fig. 1.—Height of plants from 21st March to 19th June. For explanation of symbols see text.

desirable to maintain the whole population at about the same "physiological age" during this period; this was accomplished by watering the controls with tap water and not with nitrogen. In the controls nitrogen was leached from the sand cultures; so that growth was retarded in the controls by temporary nitrogen deficiency, and in the treated plants also through drought. On 13th May, when all the plants were watered and treated with nitrogen, their heights still fell into "high nitrogen" and "low nitrogen" categories. Frequent readings of height were taken after this in order to trace the curves of recovery from drought. From an inspection of these curves (14th May to 19th June) the following comments can be made:

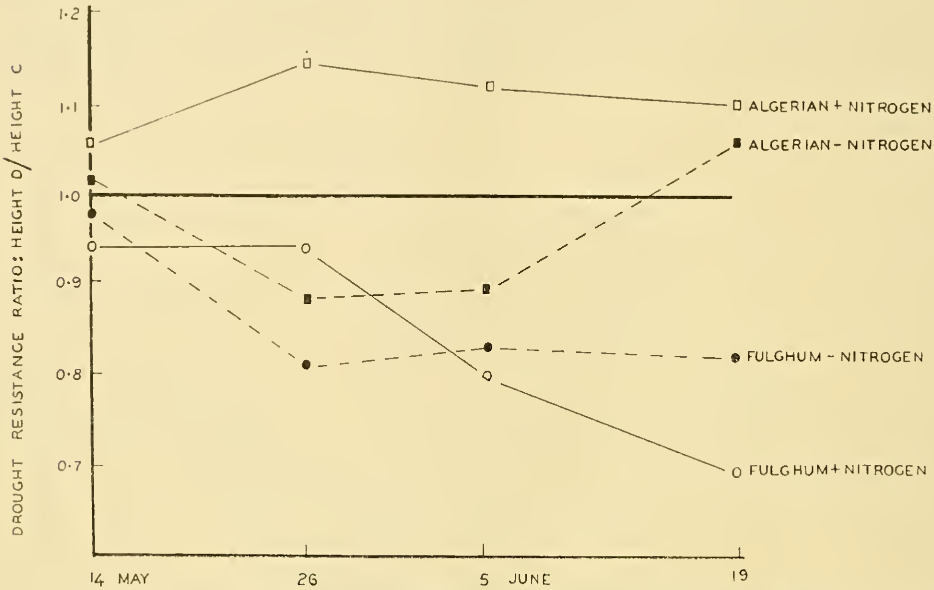
(*a*). Fulghum (controls) grew more rapidly and over a longer period than Algerian (controls).

(*b*). There is no striking difference between the recovery curves of drought and control Algerian oats, but there is a notable difference between the recovery curves of drought and control Fulghum; in other words Algerian has suffered from the drought less seriously than Fulghum.

(*c*). The "physiological maturity" of Algerian (fully manured and watered) as estimated from the shape of the growth curve, is reached early in June, whereas Fulghum is still growing rapidly in mid-June. The suggestion may be made, and it

is not inconsistent with the statistical analysis, that the superior drought resistance of Algerian in this experiment is related to its earlier physiological maturity, i.e., the higher the growth rate, the greater is the susceptibility to drought.

(*d*). Drought resistance should be measured not in terms of absolute recovery but in terms of recovery relative to the control. In Text-figure 2 the data for drought resistance are set out in this way.



Text-fig. 2.—Ratio of height of plant subjected to drought to that of control. Note that damage to Fulghum through drought increases with time, whereas in Algerian there is no evidence of damage due to drought.

(*e*). The deleterious effect of drought persists, and indeed increases, after the drought is over. Even five weeks after watering was resumed those plants of Fulghum which were subjected to drought were growing less rapidly than the controls.

A statistical analysis of the data yields further information. Details of the treatment are given in an appendix; in Table 2 the results of the analysis of growth after the drought are summarized. A further analysis into linear, quadratic and cubic components of the variance of real figures (not logarithms) revealed no features of biological interest beyond those already evident from the text-figures. The biological interpretation of the results set out in Table 2 is as follows:

TABLE 2.

Summary of significance of variables and interactions in the growth of Algerian and Fulghum oats, with high and low levels of nitrogen, after drought. Data calculated from the logarithms of readings of height. S = 99 per cent. significance ; s = 95 per cent. significance.

	May.			June.			
	14	20	26	1	7	13	19
Variables :							
Variety	s	S	S	S	S	S	S
Nitrogen	S	S	S	S	s	s	s
Drought	—	—	—	s	s	S	S
First order interactions :							
Variety × Nitrogen	—	—	s	s	—	—	—
Variety × Drought	—	s	s	s	S	S	S
Nitrogen × Drought	—	—	s	—	—	—	—

(*a*). *Variety*: A differential growth rate between varieties is a common phenomenon. Its interest here is that the relatively vigorous growth of Fulghum after 14th May may be the immediate cause of its having a lower drought resistance than Algerian.

(*b*). *Nitrogen*: The experiment was so arranged that half the plants showed symptoms of nitrogen deficiency before the drought began, and all were given an adequate supply of nitrogen after the drought was over. The odds in favour of a significant effect were reduced by this late application of nitrogen, but on 19th June they still remain greater than 95:5. An initial mineral deficiency is not offset by a late application of fertilizer; this is a familiar fact in practical agriculture.

(*c*). *Drought*: It is noteworthy that the effect of drought on the subsequent behaviour of the plant is not significant until two weeks after watering is resumed; and that thereafter significance increases with time.

(*d*). *Variety* × *Nitrogen*: There is a specific varietal response to nitrogen, in favour of Fulghum, analogous to that observed by Gregory and Crowther (1928, 1931) for barley.

(*e*). *Variety* × *Drought*: The differential effect of drought on the two varieties is evident from Text-figure 2; the analysis shows that this difference is significant and continues to increase after drought is over. Algerian suffers less than Fulghum from drought, probably on account of its lower relative growth rate, and quite apart from any advantage conferred by the root system, a factor eliminated in this experiment.

(*f*). *Nitrogen* × *Drought*: Since the subject of these studies is the effect of mineral elements on drought resistance it would be premature to discuss at this stage the influence of nitrogen. It is sufficient to point out that on one occasion (26th May) there was a significant interaction of nitrogen and drought resistance. The indication is that a high level of nitrogen (perhaps through its effect on the growth rate) renders the variety Fulghum more susceptible to the harmful effects of drought. A statistical analysis of the dry weight data (collected on 11th April and 12th May) confirms this.

In conclusion, it appears that the method of measuring drought resistance by rate of growth after drought has various advantages over the methods used hitherto. Frequent observations of shoot length are easy to take; recovery after drought is a feature of crop behaviour with which the agriculturist is concerned; the experiments require no elaborate apparatus, and they provide data which can be subjected to statistical analysis.

Summary.

1. A method of studying drought resistance is described which involves the measurement of the rate at which growth is resumed and continued after drought.

2. The method is applied to an experiment on the effect of high and low nitrogen levels on the drought resistance of two varieties of oats (Algerian and Fulghum) in sand cultures.

3. Analysis of the data shows that there is a significant effect of drought on the recovery rate, depending upon variety and nitrogen level. The details of the analysis are set out in Table 2. The data indicate that drought resistance is an inverse function of the growth rate.

Acknowledgement.

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APPENDIX.

Statistical Treatment.

Data of plant height during growth after drought were subjected to analysis of variance. Since it is desirable to work with observations at equal time intervals the only readings used were those for the following dates: 14th, 20th, 26th May, 1st, 7th, 13th, 19th June. The data for three of these occasions are interpolations but this does not affect the validity of the analysis.

Owing to damage to plants in one pot through accident, and in order to retain the symmetry of the analysis, the missing plot technique had to be applied. There were nine plants in each plot, and there was considerable variation between individuals owing to competition within the pot. Accordingly the unit selected for analysis was not the individual plant's height but the sum of the mean heights per pot in the three pots of each treatment. Variation within treatments was estimated from the data from different blocks.

The variance of plant height increases with time; it was necessary therefore to work with the logarithms of height and not with the original data. The results of the ordinary analysis of variance are summarized in Table 2 in the text. In addition an analysis using the long term experiment technique of Cochran (1939) was carried out and the interactions partitioned by the use of orthogonal functions, but the results of this analysis added nothing to the conclusions already drawn.

The data for dry weight collected on 11th April and 12th May were subjected to an ordinary analysis of variance; again a row of three pots was considered as a unit. The only significant effect on 11th April was nitrogen; on 12th May variety, nitrogen and the interaction of nitrogen and drought all reached significance.